# "On a Criterion which may serve to Test various Theories of Inheritance." By KARL PEARSON, F.R.S., University College, London. Received March 4,—Read March 17, 1904.

(1) One of the most difficult problems in the treatment of heredity is that of obtaining a satisfactory criterion which will enable us to distinguish the truth or falsehood of various hypotheses. As a rule, all the criteria used have been based upon a determination of the type of offspring due to parents of selected types. Unfortunately such a method of approaching the problem of heredity fails wholly to reach some of the most important modern theories, for the reason that these theories start from the assumption that the type of the offspring is not any, or at least any precise and simple function of the parental types. The type is said to be a factor which at present can only be determined by direct observation or by experimental crossing.

Mr. Galton in his 'Natural Inheritance,' it is true, used the term "midparent" to denote an individual compounded, in a simple way, from the two parental types, and giving offspring of a definite type. In generalising, however, Mr. Galton's conceptions in my "Law of Ancestral Heredity,"* I purposely placed before myself the aim of reducing the theory to a purely statistical theory, and discarded entirely the conception that the type of offspring was settled by the parental types. The generalised midparent of any generation became a compound of the *deviations* from type of the ancestry of that generation, and no assumption was made as to any inheritance of absolute type; the theory became purely a statistical theory of the distribution in various generations of the deviations from type. At a somewhat later date the Mendelians gave up the conception that the type of the offspring was known from the parental types. The actual effect of crossing two individuals was compared to the formation of a chemical compound, the character of which could not *à priori* be predicted from the known nature of the components. It was a matter to be determined by observation or experiment only. With this wider view the original Mendelian theory of "dominant" and "recessive" characters has disappeared, and that theory has thus far approximated itself to the "Ancestral Law."

In a second paper communicated to the Royal Society† entitled the "Law of Reversion," I endeavoured to work out a general theory of alternative inheritance, on the hypothesis that a certain number of the offspring were for any character like one or other parent or like some one or other ancestor, the proportions of offspring like ancestral types diminishing in number with the distance of descent. This

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* 'Roy. Soc. Proc.,' vol. 62, pp. 387 and 388.

† 'Roy. Soc. Proc.,' vol. 66, p. 142 *et seq.*

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theory was developed with special reference to certain characters in man and hound, which were said to be alternative, *i.e.*, the offspring, if the parental types were different, took after one or other parent. Quite recently Dr. Franz Boas* has published a very suggestive paper on "Heredity in Head Form." He propounds a theory that the cephalic index in man is a case of alternative inheritance, and that the offspring take after one or other parent. His theory is less general than my theory of 1899, because he excludes from consideration the reversion to grandparents or higher ancestry. It is more general than mine, in that he assumes imperfect and not perfect correlation between the groups of offspring and the individual parents whom they respectively follow. This I consider a distinct gain. But the neglect of ancestry, other than the immediate parents, renders the application of his theory to so-called Mendelian phenomena absolutely impossible. Thus, when a white mouse is crossed with a grey mouse the hybrid generation can hardly be considered as made up of two groups taking respectively after white and grey parents. In the following, or segregating generation, it is possible to consider the groups as a result of reversion to grandparental or higher ancestral types; it is not possible to deal with them on Dr. Boas's more limited theory. Hence, I think he errs in terming his theory a generalised form of Mendel's Law. It is a theory of alternative inheritance, and no such theory which stops at resemblance to the paternal and maternal types can describe the fundamental phenemenon of segregation in the second generation. We must deal with reversion to higher ancestors, whether such reversion be physiologically brought about by the purity of the gamete or by any other process.

A general theory of alternative inheritance may cover Mendelian phenomena; a theory of the individual dominance of either parent in one or another group of offspring, a theory of what I have defined as intermittent unit prepotency, cannot do so.† Still, Dr. Boas considers that he has evidence for his theory in the inheritance of cephalic index in man, and it seems to me that his paper indicates the manner in which it may be possible to still further generalise my results of 1899. It is clear, however, that we badly need some criterion to distinguish between these competing theories in the case of measurements of the inheritance of any given character. Since none of the three theories referred to is essentially based on the determination of the type of the offspring from the parental types,‡ we are thrown back

* 'The American Anthropologist' (N.S.), vol. 5, pp. 530—538.

† 'Biometrika,' vol. 2, p. 389.

‡ Dr. Boas, I think, has not fully understood my theory of the midparent. He repeatedly speaks of the *mid* parental value of a character and of the offspring clustering round this value on the theory of "Galton and Pearson." There is absolutely no antagonism between my theory and the stature of Americo-European half-bloods exceeding both parental types. My midparent is based solely on

on a consideration of the variability of the offspring due to parents of given types. Luckily the three theories give us totally different values of the variability of an array of offspring due to parents of given types, and we have in this question of variability a crucial test of the applicability of one or other of the theories to the inheritance of a given character.

In order to bring this point out I must briefly consider the variability of arrays of offspring under the three theories.

(2) Variability of an array of offspring on the pure statistical theory developed as the "Law of Ancestral Heredity."

If $\sigma_c$ be the standard deviation of the offspring, say of one sex, $\rho_{fc}$ their correlation with father, $\rho_{mc}$ with mother and $\rho_{fm}$ the coefficient of assortative mating, then

$$\Sigma = \sigma_c \sqrt{\left(\frac{1 - \rho_{fc}^2 - \rho_{mc}^2 - \rho_{fm}^2 + 2\rho_{fc}\,\rho_{mc}\,\rho_{fm}}{1 - \rho_{fm}^2}\right)}$$

is, whatever be the nature of the frequency distribution provided the regression be linear, the mean of the standard deviations of all the arrays due to parents of given types. If the characters be distributed according to the normal law of deviation, then $\Sigma$ will not only be the mean of all the array standard deviations, but the actual standard deviation of each array. If, therefore, the character selected be in each generation distributed according to the normal law, we should expect to find that if we take all pairs of given types, the offspring due to such pairs will have a variability given with reasonable closeness by the above result. If we deal with all the offspring due to fathers, say, of a given type, the mean standard deviation of the arrays will be $\sigma_c \sqrt{(1 - \rho_{fc}^2)}$, and in so far as the distributions are approximately normal the standard deviations of all arrays will be the same.* Hence arises the importance, when we use $\Sigma$ as the variability of the offspring, of showing that the regression for the given character is linear, and that the frequency is not widely divergent from a normal distribution. These points were dealt with by Mr. Galton in his very first investigation of the subject. He actually considered in the case of stature whether some of the offspring followed the father and some the mother, and showed that $\Sigma$ did not vary sensibly from array to array.† Subject, therefore, to a demonstration for each character that the frequency is approximately normal and the regression linear, we see that the purely statistical theory of

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deviations from type ('Roy. Soc. Proc.,' vol. 62, p. 387), and the offspring type itself may be wholly different from both parental types, exceeding or falling short of them.

* The property that $\Sigma$ is the mean of the standard deviation of all the arrays was first stated by Yule, 'Roy. Soc. Proc.,' vol. 60, p. 477, for the case of linear regression.

† 'Natural Inheritance,' pp. 89—90, and Table 10, p. 207. This investigation seems to have escaped Dr. Boas, see *loc. cit.*, p. 530.

heredity summed up in the "Law of Ancestral Heredity" would assert that the offspring of all parents of a given type would have a constant variability, whatever that type might be.

(3) *Mendel's Theory.*—If we take as a fair sample of this theory the generalised Mendelian theory, discussed by me in a recent communication to the Society, and now published in the 'Phil. Trans.,' we find that this constancy of the standard deviation of the array is no longer true. It only becomes true if the number of Mendelian couplets on which the character depends is indefinitely great. In other cases, while $\sigma_c \sqrt{(1-\rho_{fc}^2)}$ is still the mean of the standard deviations of the arrays, the actual value of the standard deviation alters sensibly and continuously as we cross the correlation table, always tending to increase in one direction and decrease in the other. Clearly we have, as I have pointed out in the paper referred to, an excellent criterion here between the two theories.*

(4) Lastly, let us turn to the theory of individual parental dominance. I will give the analysis for this case, extending and generalising Dr. Boas's formulæ. I suppose the total offspring $n$ of a pair of parents to be divided into two groups $n_1$ and $n_2$ in number. In the first groups with a mean $m_1$ the fathers are considered as predominant without the mothers being supposed at present entirely without influence; in the second group with mean $m_2$, the mothers are supposed to have the predominating influence. We may speak of these two groups, for convenience only, as "father's offspring" and "mother's offspring." Let $\sigma_{c_1}$ and $\sigma_{c_2}$ be the standard deviations of "father's offspring" and "mother's offspring" for a given character $z$; let $\sigma_f$, $\sigma_m$, $\sigma_c$ be the standard deviations of the fathers for the same character, of the mothers, and of the offspring as a whole. The mean $m$ of the offspring as a whole will be given by $m = (n_1 m_1 + n_2 m_2)/n$. Further let $r_{1f}$, $r_{2f}$ be the paternal offspring correlations for "father's offspring" and "mother's offspring," and $r_{1m}$, $r_{2m}$ the maternal offspring correlations for the same two groups respectively; $r_{fm}$ shall be the coefficient of assortative mating between parents, $x$, $y$, $z$ are the characters in father, mother, and child, $x$ and $y$ being measured from the parental means and $z$ from some other origin. Then, if $S_1$ stands for a summaration of all the offspring of the first and $S_2$ of the second class, we have

$$n\sigma_c^2 = n_1 \{\sigma_{c_1}^2 + (m_1 - m)^2\} + n_2 \{\sigma_{c_2}^2 + (m_2 - m)^2\},$$

or

$$\sigma_c^2 = (n_1\sigma_{c_1}^2 + n_2\sigma_{c_2}^2)/n + n_1 n_2 (m_1 - m_2)^2/n \quad \ldots\ldots\ldots\ldots \quad \text{(i)}.$$

Let $\rho_{fc}$ and $\rho_{mc}$ be the total paternal and maternal correlations; we have

$$\begin{aligned}\rho_{fc} &= [S_1 \{x(z-m)\} + S_2 \{x(z-m)\}]/(n\sigma_f\sigma_c)\\ &= (n_1\sigma_f\sigma_{c1}r_{1f} + n_2\sigma_f\sigma_{c_2}r_{2f})/(n\sigma_f\sigma_c),\end{aligned}$$

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* 'Phil. Trans.,' A, vol. 203, p. 66.

or

$$\rho_{fc} = \frac{n_1}{n}\frac{\sigma_{c_1}}{\sigma_c} r_{1f} + \frac{n_2}{n}\frac{\sigma_{c_2}}{\sigma_c} r_{2f} \ldots\ldots\ldots\ldots\ldots\ldots \quad \text{(ii)}.$$

Similarly,

$$\rho_{mc} = \frac{n_1}{n}\frac{\sigma_{c_1}}{\sigma_c} r_{1m} + \frac{n_2}{n}\frac{\sigma_{c_2}}{\sigma_c} r_{2m} \ldots\ldots\ldots\ldots\ldots\ldots \quad \text{(iii)}.$$

Here we have supposed that although the fathers of "father's offspring" and of "mother's offspring" will, when weighted with their offspring, be unequal in number (*i.e.* $n_1$ and $n_2$), yet their variabilities are the same, and similarly for the mothers. This is equivalent to supposing no correlation between the dominant effect of a parent and his or her deviation from type. Otherwise we cannot put $\sigma_f$ in the $S_1$ sum the same as $\sigma_f$ in the $S_2$ sum.

We are now able to write down the general regression equation of bi-parental inheritance, *i.e.*,

$$z_p - m = \frac{\rho_{fc} - \rho_{fm}\rho_{mc}}{1 - \rho^2_{mf}} \frac{\sigma_c}{\sigma_f} x + \frac{\rho_{mc} - \rho_{fm}\rho_{fc}}{1 - \rho^2_{fm}} \frac{\sigma_c}{\sigma_m} y,$$

where $z_p$ is the probable value of the character in offspring of parents of characters $x$ and $y$. Hence, if we remember that $r_{fm} = \rho_{fm}$, we have on substituting from (ii) and (iii):—

$$z_p = m + \left(\frac{n_1}{n}\frac{\sigma_{c_1}}{\sigma_f} R_{1f} + \frac{n_2}{n}\frac{\sigma_{c_2}}{\sigma_f} R_{2f}\right) x + \left(\frac{n_1}{n}\frac{\sigma_{c_1}}{\sigma_m} R_{1m} + \frac{n_2}{n}\frac{\sigma_{c_2}}{\sigma_m} R_{2m}\right) y \ldots \quad \text{(iv)},$$

where $R_{1f}$, $R_{1m}$ are the bi-parental co-efficients $(r_{1f} - r_{mf}\, r_{1m})/(1 - r_{mf}^2)$ and $(r_{1m} - r_{mf}\, r_{1f})/(1 - r_{mf}^2)$, of the "father's offspring" and $R_{2f}$, $R_{2m}$ similar quantities for the "mother's offspring."

Now, fixing our attention for a moment on "father's offspring," we should expect parents of characters $x$ and $y$ to produce an array of father's offspring with a mean:

$$\mu_1 = m_1 + R_{1f}\frac{\sigma_{c_1}}{\sigma_f} x + R_{1m}\frac{\sigma_{c_1}}{\sigma_m} y \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad \text{(v)},$$

and with a standard deviation $s_1$ given by

$$s_1^2 = \sigma_{c_1}^2 (1 - r_{1f}^2 - r_{1m}^2 - r_{mf}^2 + 2 r_{1f} r_{1m} r_{mf})/(1 - r_{mf}^2) \quad \ldots \quad \text{(vi)}.$$

Similarly the arrays of "mother's offspring" for parents of the same characters would have a mean:

$$\mu_2 = m_2 + R_{2f}\frac{\sigma_{c_2}}{\sigma_f} x + R_{2m}\frac{\sigma_{c_2}}{\sigma_m} y \ldots\ldots\ldots\ldots\ldots\ldots \quad \text{(vii)},$$

and a standard deviation $s_2$ given by

$$s_2^2 = \sigma_{c_2}^2 (1 - r_{2f}^2 - r_{2m}^2 - r_{mf}^2 + 2 r_{2f} r_{2m} r_{mf})/(1 - r_{mf}^2) \ldots \quad \text{(viii)}.$$

Now, if $\nu_1$ and $\nu_2$ be the numbers of children in the array of $x\ y$ parents belonging to either group, and $\nu = \nu_1 + \nu_2$, we shall have for the standard deviation of the total offspring of $x\ y$ parents :

$$\nu\Sigma_{xy}^2 = \nu_1\{s_1^2 + (\mu_1 - z_p)^2\} + \nu_2\{s_2^2 + (\mu_2 - z_p)^2\} \quad \ldots\ldots \quad \text{(ix)},$$

where $z_p$ is given by (iv) and is the mean of the whole array.

If the relative influences of mother and father depended upon their characters, we could go no further with (ix) until this had been determined. If, however, we suppose this influence on the average to be not sensibly dependent on the characters $x$ and $y$, we may write $n_1/n = \nu_1/\nu$ and $n_2/n = \nu_2/\nu$. Substitute from (iv), (v) and (vii), we find after some reductions:

$$\Sigma_{xy}^2 = \frac{n_1 s_1^2 + n_2 s_2^2}{n} + \frac{n_1 n_2}{n^2}\left\{(m_1 - m_2) + \left(\mathrm{R}_{1f}\frac{\sigma_{c_1}}{\sigma_f} - \mathrm{R}_{2f}\frac{\sigma_{c_2}}{\sigma_f}\right)x + \left(\mathrm{R}_{1m}\frac{\sigma_{c_1}}{\sigma_m} - \mathrm{R}_{2m}\frac{\sigma_{c_2}}{\sigma_m}\right)y\right\}^2 \quad \ldots\ldots \quad \text{(x)}.$$

To verify this equation I transferred to the mean, summed for every possible array, *i.e.*, for all values of $x$ and $y$, and divided by the total number of arrays. The left-hand side should be $\sigma_c^2$, the right-hand side became, after some considerable reductions, identical with the right-hand side of (i), as it should be.

We have in equation (x) accordingly, the variability of an array of all offspring on the hypothesis that the children may be divided into two groups, differently related to the two parents. We see at once that the variability of an array will depend on the actual values of the parental characters, unless :

$$\mathrm{R}_{1f}\sigma_{c_1}/\sigma_f = \mathrm{R}_{2f}\sigma_{c_2}/\sigma_f,$$

and

$$\mathrm{R}_{1m}\sigma_{c_1}/\sigma_m = \mathrm{R}_{2m}\sigma_{c_2}/\sigma_m.$$

But this is asserting that the bi-parental regression co-efficients for the two groups are the same, or, as we may put it, that there is no distinction between the parental influences in the two groups. This is the case usually assumed under the "Law of Ancestral Heredity" with its constant variability within the limits of random sampling for the arrays. In every other case the arrays alter in variability with the magnitude of the parental character.

Let us look at the matter from another light and sum $\Sigma^2_{xy}$ for every value of $y$ only, or we can obtain the same result by direct investigation, namely, we find if $\Sigma_x$ be the standard deviation of an array of offspring due to fathers of character $x$,

$$\Sigma_x^2 = \frac{n_1\sigma_{c_1}^2(1 - r_{1f}^2) + n_2\sigma_{c_2}^2(1 - r_{2f}^2)}{n} + \frac{n_1 n_2}{n^2}\left\{m_1 - m_2 + \left(r_{1f}\frac{\sigma_{c_1}}{\sigma_f} - r_{2f}\frac{\sigma_{c_2}}{\sigma_f}\right)x\right\}^2 \quad \ldots\ldots \quad \text{(xi)}.$$

Or, we see that unless

$$r_{1f}\sigma_{c_1}/\sigma_f = r_{2f}\sigma_{c_2}/\sigma_f,$$

*i.e.*, the paternal influence be the same in both groups, or there be no question of individual dominance of the parents in "father's offspring" and "mother's offspring" respectively, the arrays of offspring due to different classes of fathers will not be equally variable. It is clear that if the standard deviation of the array be plotted to the size of the father's character, the resulting curve will be a hyperbola with real axis vertical, and in the two directions across the correlation table taken from the parental value

$$x = (m_1 - m_2)\Big/\left(r_{2f}\frac{\sigma_{c_2}}{\sigma_f} - r_{1f}\frac{\sigma_{c_1}}{\sigma_f}\right)$$

the variability of the arrays will rapidly increase from a minimum.

As there can hardly be a sensible distinction between $m_1$ and $m_2$, for it would mean bimodality in all the characters dealt with, which is contrary to experience, we may say that the variability of the offspring arrays increases in both directions with the deviation of the father (or mother) from the mean.

If we put $m_1 = m_2$ we have :

$$\Sigma_x^2 = \frac{n_1\sigma_{c_1}^2(1 - r_{1f}^2) + n_2\sigma_{c_2}^2(1 - r_{2f}^2)}{n} + \frac{n_1 n_2}{n^2}\left(r_{1f}\frac{\sigma_{c_1}}{\sigma_f} - r_{2f}\frac{\sigma_{c_2}}{\sigma_f}\right)^2 x^2 \quad \ldots \text{(xii)}.$$

which shows clearly how the variability of the array increases hyperbolically with the deviation of the father from the mean.

(5) Now it is as well to take one or two numerical cases to appreciate the degree of curvature of this hyperbola, for if it were a very flat hyperbola, it possibly could not be readily distinguished from a horizontal straight line (Ancestral Law) or from a parabola (Mendel's Law). I take the hypothesis suggested by Dr. Boas, *i.e.*, a negligible influence of the father on "mother's offspring," and a negligible influence of the mother on "father's offspring."

We have $r_{2f} = r_{1m} = 0$. Further, if we suppose the two groups of offspring to be equal in number and equally variable, $n_1 = n_2$ and $\sigma_{c_1} = \sigma_{c_2} = \sigma_c$. From (ii) it follows that

$$\rho_{fc} = \frac{n_1}{n}\frac{\sigma_{c_1}}{\sigma_c} r_{1f} = \tfrac{1}{2} r_{1f}.$$

Therefore from (xii) it follows that

$$\Sigma_x^2 = \sigma_c^2\left\{(1 - 2\rho^2_{fc}) + \rho_{fc}^2\frac{x^2}{\sigma_f^2}\right\}.$$

Accordingly, we have:

$$
\begin{aligned}
x &= 0, & \Sigma_x^2 &= \sigma_c^2(1-2\rho_{fc}^2),\\
x &= \sigma_f, & \Sigma_x^2 &= \sigma_c^2(1-\rho_{fc}^2),\\
x &= \sqrt{2}\sigma_f & \Sigma_x^2 &= \sigma_c^2,\\
x &= 2\sigma_f, & \Sigma_x^2 &= \sigma_c^2(1+2\rho_{fc}^2),
\end{aligned}
$$

whence we have the following table:—

Table of $\Sigma_x/\sigma_c$.

| | $\rho_{fc}$. | | |
|---|---|---|---|
| $x$. | 0·3. | 0·4. | 0·5. |
| 0......... | 0·91 | 0·82 | 0·71 |
| $\sigma_f$........ | 0·95 | 0·96 | 0·87 |
| $\sqrt{2}\sigma_f$..... | 1·00 | 1·00 | 1·00 |
| $2\sigma_f$....... | 1·09 | 1·15 | 1·22 |

Now parental correlations in my experience of extensive masses of good data are rarely as low as 0·3, generally over 0·4, or nearer even 0·5. But even with 0·3 we see that there ought to be about 20 per cent. increase in the standard deviation of an array as we pass from the mean father to a father with a deviation equal to twice the paternal deviation, *i.e.*, to an array which will be given with at least a moderate number of cases in any parental correlation table. As we approach a parental correlation of 0·4—0·5, this increase of the standard deviation amounts to 40—72 per cent., and should be still more conspicuous. We conclude, therefore, that if the parents are respectively dominant in two separate groups of offspring, then when we plot the standard deviations of the arrays of offspring to the deviations of the parent from the mean, we ought to get a very sensibly hyperbolic curve. Or, if we plot the squares of the one to those of the other, we ought to get a sloping straight line of very sensible slope, 0·1—0·25 about, instead of the horizontal line of the "Ancestral Law."

If we suppose the same conditions to apply to a bi-parental array, *i.e.*, $m_1 = m_2$, $n_1 = n_2 = \frac{1}{2}n$, $\sigma_{c_1} = \sigma_{c_2} = \sigma_c$, $r_{2f} = r_{1m} = 0$, we find that (x) reduces to

$$\Sigma_{xy}^2 = \sigma_c^2\left\{\left(1-\frac{1}{2}\frac{r_{1f}^2+r_{2m}^2}{1-r_{mf}^2}\right)+\left(\frac{\frac{1}{2}r_{1f}}{1-r_{mf}^2}\frac{x}{\sigma_f}-\frac{\frac{1}{2}r_{2m}}{1-r_{mf}^2}\frac{y}{\sigma_m}\right)^2\right\}.$$

Or, using (ii) and (iii), which give $\rho_{fc} = \frac{1}{2}r_{1f}$, $\rho_{mc} = \frac{1}{2}r_{2m}$:

$$\Sigma_{xy}^2 = \sigma_c^2\left\{\left(1-2\frac{\rho_{fc}^2+\rho_{mc}^2}{1-\rho_{mf}^2}\right)+\left(\frac{\rho_{fc}}{1-\rho_{mf}^2}\frac{x}{\sigma_f}-\frac{\rho_{mc}}{1-o_{mf}^2}\frac{y}{\sigma_m}\right)^2\right\} \quad \text{(xiii)}.$$

Let us apply this to the case of stature of parents and sons in man. Here I have deduced from my "Family Data Records"*

$$\rho_{fc} = 0\cdot5140,\ \rho_{mc} = 0\cdot4938,\ \rho_{mf} = 0\cdot2804\ldots\ldots\ldots \quad \text{(xiv)}.$$

We find:

$$\Sigma_{xy}^2/\sigma_c^2 = -0\cdot1028 + \left(0\cdot5579\,\frac{x}{\sigma_f} - 0\cdot5359\,\frac{y}{\sigma_m}\right)^2 \ldots\ldots \quad \text{(xv)}.$$

Hence we have the impossible value $32\sigma_c\sqrt{-1}\,\sigma_c$ for the variability of the arrays of offspring due to mean .parents. Generally we deduce—

Values of $\Sigma_{xy}/\sigma_c$ for Arrays.

| Father: $x/\sigma_f$. | Mother: $y/\sigma_m$. | Array: $\Sigma_{xy}/\sigma_c$. |
|---|---|---|
| 0 | 0 | (0·32 √(−1) ?) |
| +1 | 0 | 0·46 |
| +1 | −1 | 1·05 |
| +1 | −2 | 1·60 |
| +2 | −2 | 2·19 |

We are dealing here with measurements on upwards of 1000 families; the probable errors, therefore, of $\rho_{fc}$ and $\rho_{mc}$ hardly allow of our supposing the first term on the right in (xiv) to be zero. But if we do make this hazardous assumption, we see that as we pass from pairs of mean parents to fathers of 6′ 1″ and mothers of 4′ 10″ we should pass from an array of offspring of no variability to one *twice* as variable as the general population. Further, for any given male there would exist a female relatively only very slightly taller than he is, who would have offspring with him of sensibly no variability. In view of this result we may safely assert that the hypothesis of "father's offspring" and "mother's offspring" cannot apply to stature in man under any conditions in the least approximating to Dr. Boas's assumptions in the case of cephalic index.

(6) Our conclusions may be summed up as follows:—The variability of the array of offspring due to a group of parents of definite character can be satisfactorily used as a criterion between various theories of inheritance. In particular if the variability of the array be plotted to the character of the parent—

(*a*) On the hypothesis of the "Ancestral Law" a horizontal straight line is the resulting curve.

(*b*) On the generalised Mendelian theory the result is a parabola with horizontal axis.

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* 'Biometrika,' vol. 2, pp. 373 and 378.

(*c*) On the generalised theory of alternative inheritance which divides the offspring into two groups more intimately associated with one or other parent, the resulting curve is a hyperbola with vertical real axis.

(7) I have applied the criterion here developed to my measurements on father and son in more than 1000 families. The three characters stature, span and forearm are dealt with. The correlation tables for the paternal inheritance of these characters will be found in a recent memoir by Dr. Lee and myself on the "Inheritance of the Physical Characters in Man."* We excluded all arrays with less than eight individuals in them, deeming it absolutely untrustworthy to find a mean and standard deviation from fewer than eight cases. The standard deviation of each array for a given paternal character was found by Dr. Alice Lee. These were then plotted to the paternal character by Mr. W. L. Atcherley, and results are shown in the accompanying Diagram 1. The zigzag polygons in each case give the plotted variabilities of the arrays, the vertical numbers being the total on which the variability is based. The horizontal line AA gives the mean value, $\sigma_c \sqrt{(1-\rho_{fc}{}^2)}$, of the standard deviations of the arrays according to the statistical theory. The broken lines *ccc* and *c′c′c′* give $\sigma_c \sqrt{(1-\rho^2{}_{fc})} \pm$ twice the probable error of the deviation of an array from $\sigma_c \sqrt{(1-\rho^2{}_{fc})}$. Thus if $\Sigma = \sigma_c \sqrt{(1-\rho^2{}_{fc})}$ and $\Sigma_x =$ the standard deviation of an array of $m$ individuals out of a total of $n$, we have plotted up and down from $\Sigma$ the quantity

$$2 \times 0{\cdot}65449 \sqrt{\left(\frac{\Sigma^2}{2n} + \frac{\Sigma_x{}^2}{2m}\right)}.$$

Now unless a difference is at least *twice* its probably error we certainly cannot assert it to be significant. Now, if the diagram be examined, it will be seen that almost without exception the zigzag polygons fall well within the non-significant areas bounded by *ccc* and *c′c′c′*. There are, indeed, three exceptions, but all three occur in arrays with less than twenty individuals, or arrays where some eccentricity of individual or measurement might easily make itself felt. But there is really no need to appeal even to this explanation, we have thirty-nine observations on arrays, and three of these only exceed the double of their probable error; this is actually less than *half* the excesses we might have expected on the theory of probability.

There is clearly absolutely nothing in the observed results opposed to that constancy of variability in the arrays which is suggested in the usual treatment of the "Law of Ancestral Heredity."

(8) I next look at the theory of alternative inheritance, or at the hypothesis that some children follow the one, some the other parent. An examination of the diagrams show that there is not the least

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* 'Biometrika,' vol. 2, pp. 415—417.

approach to a hyperbolic distribution of the array variabilities. The hyperbola would have its axis vertical and vertex downwards. In the case of stature I give the hyperbola that would result from a special

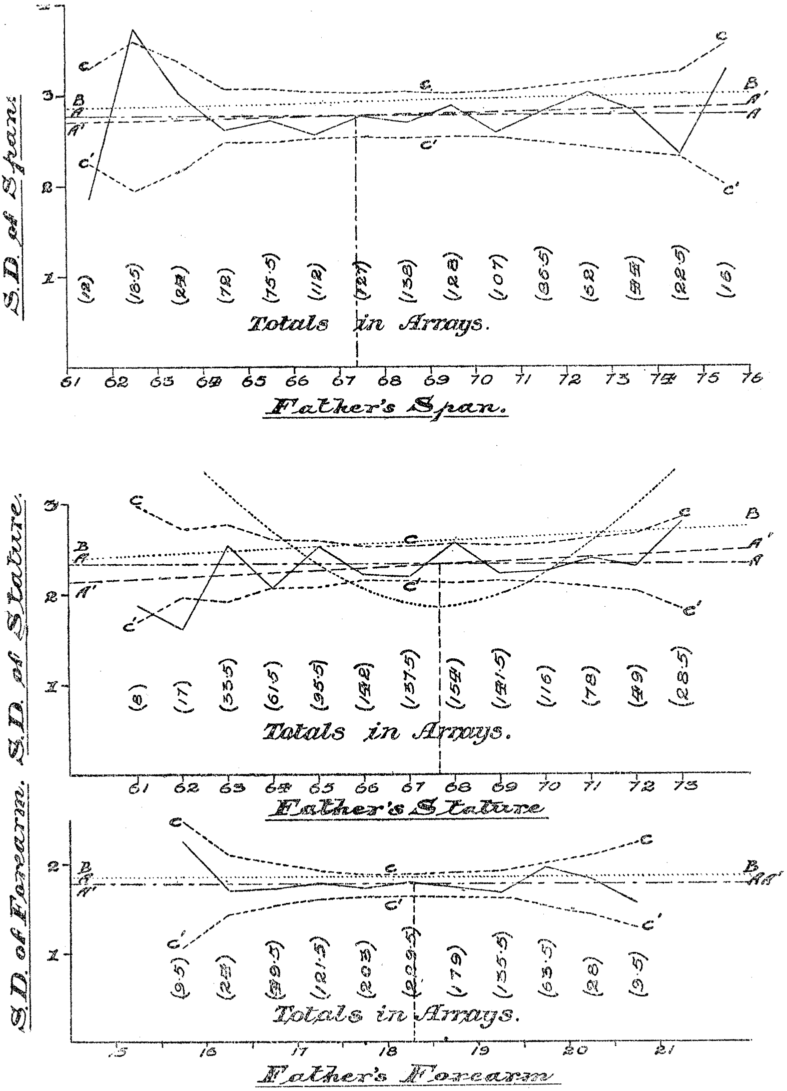

Diagram I.—Arrays of sons.

case, namely, Dr. Boas's hypothesis of equal numbers of offspring with equal variability and of like mean following each parent. The equation to this hyperbola may be found from (xi), by putting

$\sigma_{c_1} = \sigma_{c_2} = \sigma_c = 2''\cdot 710$, $r_{1f} = 2\rho_{fc} = 1\cdot 0280$, $n_1 = n_2 = \frac{1}{2}n$, and $r_{2f} = 0$. We have

$$(\Sigma_x/\sigma_c)^2 = 0\cdot 4716 + 0\cdot 2642\,(x/\sigma_f)^2,$$

where $\sigma_f = 2''\cdot 568$.

It will be seen at once that the variability of the array is too small for the mean father and far too large for the exceptional father. I think we may safely conclude that for man in the case of the three characters under investigation no such theory of alternative inheritance applies.

(9) I now turn to the third or Mendelian hypothesis. Are the variability distributions better represented by parabolas of horizontal axes than by horizontal straight lines? We have a series of points in each case and the question is: What is the best fitting parabola? The equation to the Mendelian parabola, as given in my memoir already referred to,* is in the notation of the present paper

$$\frac{\Sigma_x^2}{\sigma_c^2} = \frac{8}{9} + \frac{4}{9\sqrt{(3q)}}\,\frac{x}{\sigma_f} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad \text{(xvi)},$$

where $q$ is the number of Mendelian couplets, and $x$ is measured from the mean.† Writing $\Sigma_x^2/\sigma_c^2 = \xi$, $x/\sigma_f = \eta$, this is of the form, $a$ and $b$ being numerics:

$$\xi = a + b\eta.$$

Applying the method of least squares, since $a$ is an absolute constant, we find for the best value of $b$, $\mu_x$ being the total in the $x$ array:

$$b = \frac{\sigma_f}{\sigma_c^2}\,\frac{\mathrm{S}\,\{\mu_x\,(\Sigma_x^2 - \frac{8}{9}\sigma_c^2)\,x\}}{\mathrm{S}\,(\mu_x\,x^2)},$$

or, $q$ the number of Mendelian couplets is to be found from

$$\frac{1}{\sqrt{(q)}} = \frac{9\sqrt{(3)}}{4}\,\frac{\sigma_f}{\sigma_c^2}\,\frac{\mathrm{S}\,\{\mu_x\,(\Sigma_x^2 - \frac{8}{9}\sigma_c^2)\,x\}}{\mathrm{S}\,(\mu_x\,x^2)} \quad \ldots\ldots\ldots \quad \text{(xvii)}.$$

Working this out for the case of stature first, I found, after some rather laborious arithmetic, that $q = 48$. Thus the best fitting Mendelian parabola needs no less than 48 couplets. We may write the parabola in the form

$$\frac{\Sigma_x^2}{\sigma_c^2} = \tfrac{8}{9}\left(1 + \tfrac{1}{24}\,\frac{x}{\sigma_f}\right).$$

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* 'Phil. Trans.,' A, vol. 203, pp. 66–67.

† To reduce to the result of the above memoir we have $\Sigma_x = \epsilon\sigma_s$, $\sigma_c = \sigma_f = \epsilon\sqrt{(\frac{3}{16})n}$ $x = \epsilon(s - \frac{1}{4}n)$, $q = n$, where $\epsilon$ is an undetermined constant depending on the relation between actual scale and number of Mendelian couplets.

or, since $x$ does not exceed 2 to 3 $\sigma_f$ we have for the part of the parabola involved very nearly the straight line

$$\Sigma_x/\sigma_c = \sqrt{\tfrac{8}{9}}\left(1+\tfrac{1}{48}\frac{x}{\sigma_f}\right) \quad\ldots\ldots\ldots\ldots\ldots\ldots \quad \text{(xviii)}.$$

This, substituting the values of $\sigma_c$ and $\sigma_f$, is a straight line of slope 0·021. Now the best fitting line to the observations, A′A′, has a slope of 0·022, or we conclude that the Mendelian parabola is when the number of couplets is as large as in the present case sensibly parallel to the line which best represents the variability of the arrays plotted to the parents' character. The Mendelian line B′B′ of Diagram I is not as good a fit as the line AA′, because the theory constrains it to pass through the point given by $\sigma_s = \sqrt{(8/9)}\,\sigma_c$, and not through the actual mean point $\sigma_c\sqrt{(1-r_{fc}^2)}$. This is owing to the fact that the Mendelian theory gives $r_{fc}$ constant and equal to 1/3. Hence, we see that the Mendelian theory will not, as a rule, give as good a fit to the observations as the best fitting line, when the number of couplets is large as in this case and the correlation differs from 1/3. The parabola thus sensibly coincides in direction with the best fitting straight line, but is raised above it in position.

I give the best fitting straight lines for the three characters we have been considering

*For Span*—

$$y - 2''{\cdot}762 = 0{\cdot}011\,(x - 67''{\cdot}396).$$

Probable error of the slope 0·011, equals 0·013.

*For Stature*—

$$y - 2''{\cdot}344 = 0{\cdot}022\,(x - 67''{\cdot}686).$$

Probable error of the slope 0·022, equals 0·013.

*For Forearm*—

$$y - 1''{\cdot}773 = -0{\cdot}003\,(x - 18''{\cdot}279).$$

Probable error of the slope −0·003, equals 0·009.

Thus, of the three slopes all differ by less than twice and two of them by less than once their probable error from zero. We may accordingly conclude that neither in the best fitting straight lines, nor consequently in the Mendelian parabolas for the measurable range, is there any sensible deviation from horizontality. In fact we have 48 couplets in the case of stature, and roundly 150 for span* and 2000 for forearm. With such numbers the Mendelian theory cannot on the problem of variability of arrays give any other sensible answer for the range available for investigation than the constant variability of the "Ancestral Law," but it does not equal the latter law in its description of the facts, because it shifts the mean variability of the array out of its proper place owing to its absolute rigidity in the value of parental correlation. I think we may say that for the three characters here considered the "Law of Ancestral Heredity" is the only one of the three theories which clearly describes the facts, and the facts at no point differ significantly from its statements.

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* If the Mendelian theory discussed were correct, it would be difficult to grasp how the forearm-inheritance could be determined by far *more* couplets than the span is, or why one slope should be negative and the other positive.

(10) The theory of alternative inheritance, which differentiates the offspring into "father's offspring" and "mother's offspring," permits of being tested in another manner, namely, by considering the variability of the array of brothers who have a brother of given character $x$. Let us first look at the problem generally. A man of extreme character value will have a group of brethren, say, "father's offspring," who allowing for regression are like himself, but the other group of his brethren will be far less like himself, and on the average of all mothers near the population mean. Thus, the array of brethren of a man of extreme character will be made up of two components, one tending to be like himself, the other like the general population. Hence on the whole the array of brothers corresponding to men of a given type must become more and more variable, the more marked the deviation of the given type. I will now give the results of the analysis. Let $\rho$ be the general correlation of brothers, $m$ their mean, and $\sigma$ their standard deviation. Let $r_{11}$ be the correlation of brothers who are "father's offspring," $m_1$ their mean, and $\sigma$ their standard deviation; let $r_{22}$, $m_2$ and $\sigma_2$ be the corresponding constants for the brethren who are "mother's offspring." Let $\nu_1$ and $\nu_2$ be the number of brethren of each class. Then if an individual have a deviation $x$ from the mean of all brethren, he will if a "father's offspring" have a co-fraternity of standard deviation $\sigma_1 \sqrt{(1-r_{11}^2)}$ and at distance from the mean of offspring given by

$$\begin{aligned}\mu_{11} &= m_1 + r_{11}\frac{\sigma_1}{\sigma_1}(x + m - m_1) - m - \rho x \\ &= (r_{11} - \rho)\,x + (m_1 - m)(1 - r_{11}).\end{aligned}$$

He will have $\nu_1 - 1$ of such brethren, but he will also have $\nu_2$ brethren of mother's offspring type with a standard deviation $\sigma_2 \sqrt{(1-r_{12}^2)}$ and at distance from mean of offspring given by

$$\begin{aligned}\mu_{12} &= m_2 + r_{12}\frac{\sigma_2}{\sigma_1}(x + m - m_2) - m - \rho x \\ &= \left(r_{12}\frac{\sigma_2}{\sigma_1} - \rho\right)x + (m_2 - m)(1 - r_{12}).\end{aligned}$$

Similarly, if the brother of deviation $x$ were a "mother's offspring," his brethren would be made up of $\nu_2 - 1$ of standard deviation $\sigma_2 \sqrt{(1-r_{22}^2)}$ and mean $\mu_{22}$, and of $\nu_1$ brethren of standard deviation $\sigma_1 \sqrt{(1-r_{12}^2)}$ and mean $\mu_{21}$ where

$$\mu_{22} = (r_{22} - \rho)\,x + (m_2 - m)\,(1 - r_{22})$$

$$\mu_{21} = \left(r_{12}\frac{\sigma_1}{\sigma_2} - \rho\right)x + (m_1 - m)\,(1 - r_{12}).$$

Hence, generally for the variability of the brethren of a given brother of deviation $x$, we have

$$\begin{aligned}\Sigma_x{}^2 = \sigma_1{}^2 &\left\{\frac{\nu_1 - 1}{2\,(\nu_1 + \nu_2 - 1)}\,(1 - r_{11}{}^2) + \frac{\nu_1}{2\,(\nu_1 + \nu_2 - 1)}\,(1 - r_{12}{}^2)\right\}\\ + \sigma_2{}^2 &\left\{\frac{\nu_2 - 1}{2\,(\nu_1 + \nu_2 + 1)}\,(1 - r_{22}{}^2) + \frac{\nu_2}{2\,(\nu_1 + \nu_2 - 1)}\,(1 - r_{12}{}^2)\right\}\\ &+ \mu_{11}{}^2\,\frac{\nu_1 - 1}{2\,(\nu_1 + \nu_2 - 1)} + \mu^2{}_{22}\,\frac{\nu_2 - 1}{2\,(\nu_1 + \nu_2 - 1)} + \mu_{12}{}^2\,\frac{\nu_2}{2\,(\nu_1 + \nu_2 - 1)}\\ &\qquad + \mu_{21}{}^2\,\frac{\nu_1}{2\,(\nu_1 + \nu_2 - 1)} \quad \ldots\ldots \quad \text{(xix).}\end{aligned}$$

Clearly this gives a hyperbola for $\Sigma_x$ in terms of $x$, with its real axis perpendicular to $x$.

Similarly we have :

$$\begin{aligned}\rho\sigma^2 = &\frac{\nu_1\,(\nu_1 - 1)}{(\nu_1 + \nu_2)\,(\nu_1 + \nu_2 - 1)}\,\{r_{11}\sigma_1{}^2 + (m_1 - m)^2\}\\ &+ \frac{\nu_2\,(\nu_2 - 1)}{(\nu_1 + \nu_2)\,(\nu_1 + \nu_2 - 1)}\,\{r_{22}\sigma_2{}^2 + (m_2 - m)^2\}\\ &+ \frac{2\nu_1\nu_2}{(\nu_1 + \nu_2)\,(\nu_1 + \nu_2 - 1)}\,\{r_{12}\sigma_1\sigma_2 + (m_1 - m)\,(m_2 - m)\} \quad \ldots\ldots \quad \text{(xx),}\end{aligned}$$

and further

$$\sigma^2 = \frac{\nu_1}{\nu_1 + \nu_2}\,\{\sigma_1{}^2 + (m_1 - m)^2\} + \frac{\nu_2}{\nu_1 + \nu_2}\,\{\sigma_2{}^2 + (m_2 - m)^2\},$$

and

$$m = \frac{\nu_1 m_1 + \nu_2 m_2}{m_1 + m_2}.$$

In any actual case we may reasonably suppose our pairs of brothers to be a random sample from families with indefinitely great numbers,* or put $\nu_1$ and $\nu_2$ infinite in the ratio of $n_1$ to $n_2$. Hence :

$$m = (m_1 n_1 + m_2 n_2)/n, \qquad \sigma^2 = (n_1\sigma_1{}^2 + n_2\sigma_2{}^2)/n + \frac{n_1 n_2}{n_2}(m_1 - m_2)^2,$$

$$\rho\sigma^2 = \frac{n_1{}^2}{n^2}\,r_{11}\sigma_1{}^2 + \frac{n_2{}^2}{n^2}\,r_{22}\sigma_2{}^2 + \frac{2n_1 n_2}{n^2}\,r_{12}\sigma_1\sigma_2 \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad \text{(xxi),}$$

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* 'Phil. Trans.,' A, vol. 203, p. 77.

$$\Sigma_x^2 = \sigma_1^2\left\{\tfrac{1}{2}\frac{n_1}{n}(1-r_{11}^2)+\frac{n_1}{2n}(1-r_{12}^2)\right\}$$

$$+\sigma_2^2\left\{\tfrac{1}{2}\frac{n_2}{n}(1-r_{22}^2)+\frac{n_2}{2n}(1-r_{12}^2)\right\}$$

$$+\frac{n_1}{2n}(\mu_{11}^2+\mu_{21}^2)+\frac{n_2}{2n}(\mu_{22}^2+\mu_{12}^2) \;\ldots\ldots\ldots\ldots\; \text{(xxii)}.$$

To simplify still further, assume no distinction in the totals of "mothers' offspring" and "fathers' offspring," or take $m_1 = m_2 = m$, $\sigma_1 = \sigma_2 = \sigma$, $n_1 = n_2 = \frac{1}{2}n$. Hence

$$\rho = \tfrac{1}{4}(r_{11}+r_{22})+\tfrac{1}{2}r_{12},$$

$$\Sigma_x^2 = \sigma^2\{1-\tfrac{1}{4}(r_{11}^2+r_{22}^2)-\tfrac{1}{2}(1-r_{12}^2)\}$$

$$+\tfrac{1}{4}\{(r_{11}-\rho)^2+(r_{22}-\rho)^2+2(r_{12}-\rho)^2\}x^2.$$

Hence we see that if the variability of the arrays of brethren is to be constant, it is absolutely necessary that $r_{11} = r_{22} = r_{12} = \rho$, or the degree of likeness between brothers whether they belong to "mothers' offspring" or "fathers' offspring" must be identical. If this be not true, the variability of the array of brethren of a brother of given character must obey a hyperbolic law, being least for a brother of mean character.

If we adopt Dr. Boas's theory of complete alternate inheritance we have

$$r_{11} = r_{22} \quad\text{and}\quad r_{12} = 0.$$

Whence

$$r_{11} = 2\rho,$$

and

$$\Sigma_x^2 = \sigma^2(1-2\rho^2)+\rho^2x^2 \;\ldots\ldots\ldots\ldots\ldots\ldots\; \text{(xxiii)}.$$

This is a very easy result to test. On the whole, however, it is better to ask the general question: Are the variability of arrays of brethren hyperbolically distributed?

(11.) I propose to answer this by appeal to my data for nearly 2000 pairs of brothers measured for their cephalic index. Selecting the arrays of 20 brothers and upwards the results plotted in Diagram II. were reached. Here $\rho = 0{\cdot}4861$ and $\sigma = 3{\cdot}314$ and the mean cephalic index $= 78{\cdot}92$. Hence the "Law of Ancestral Heredity" gives for the mean value of $\Sigma_x$, $\Sigma = 2{\cdot}896$. On Dr. Boas's hypothesis

$$\Sigma_x^2 = 5{\cdot}7924+0{\cdot}2363x^2.$$

These results are shown in the same manner as in the first diagram, the broken lines marking the limits of twice the probable error of $\Sigma$ and the actually observed $\Sigma_x$.

We may, I think, safely conclude from this result that the horizontal or mean line of the "Ancestral Law" gives a better result than the hyperbola. As a matter of fact in the small arrays at the extremes we get as before very erratic results; almost any value of the standard deviation may be reached, not only because the probable errors are so large, but because the appearance of any single abnormality or of any slip due to measurement or classification becomes so very disturbing in these small arrays. Even then we only find four cases in seventeen which deviate by more than twice the probable error from the mean line. In this case the mean error of the "Ancestral Law" for the seventeen arrays is 0·31, and of Dr. Boas's hyperbola 0·49.*

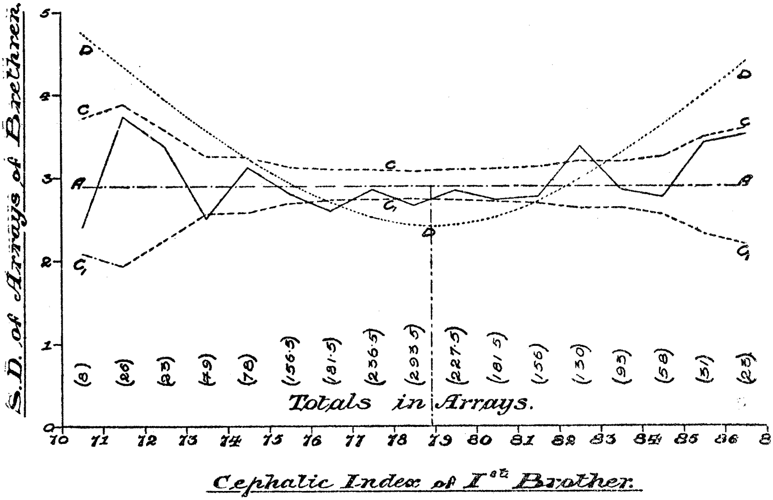

Diagram II.

(12.) It may be asked how Dr. Boas has reached the conclusion that in the case of cephalic index the "Ancestral Law" does not apply and that the children break up into "mothers' offspring" and "fathers' offspring"? He has used the measurements of Dr. Maurice Fishberg of New York, on forty-eight families of "East European Jews." Now, I think it may be reasonably questioned whether a population defined as "East European Jews" can be considered as homogeneous. I mean by this: Would any such category breed true to itself? Is it to be looked upon as a "race" in the sense used by me† of a population which has been isolated and intra-bred for some generations? If not, it would very possibly exhibit "segregation" in the second generation; thus if there were any Aryan or other non-Jewish blood in the immediate ancestry, this might be induced by a segregation tendency increasing the variability in the offspring of such pairs. Further apparent segregation would arise in the case of any unfaithfulness, and this might be correlated with physical dissimilarity. Shortly, we want a good deal further information as to the nature of these particular American East European Jews. But quite apart from all this, the forty-eight families had only 158 children or an average of less than 3·3. Now, some families must have had four and five children and Dr. Boas gives the standard deviation of all the separate families, or he must have found a standard deviation here and there on the basis of at least two and possibly even fewer individuals![*] I do not think standard deviations so found can be of any value at all. Further, and most important, he has not determined the standard deviation about the mean of the individual family, which he ought to have done, but about the theoretical average mean of all families having a father and mother of the given characters. Now the *individual* family has all its ancestors in common beside the father and mother and hence its mean is *not* in our previous notation:

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* If the large values often found for the variability of the extreme arrays of a correlation table have real significance, which I doubt, I personally am inclined to think it is due to deviation from true linear regression, the regression curve being a cubic curve with its inflexional portion representing the regression line of the ordinary range.

† 'Biometrika,' vol. 2, p. 511, and compare with the stable Mendelian population discussed in my paper, 'Phil. Trans.,' A, vol. 203, pp. 58—60.

$$m + R_{fc}\frac{\sigma_c}{\sigma_f}x + R_{mc}\frac{\sigma_c}{\sigma_m}y,$$

the value used by Dr. Boas, but the much longer expression given by the general formula for "Ancestral Heredity."[†] It is only when we take the average results for *all* families of parents $x$ and $y$, that the other ancestral terms will disappear, and we reach the above result His only method of reaching an approximation to the mean of an *individual* family, would be to actually find it from the family itself, and then investigate the standard deviation from this mean.[‡] This he has not done, and I think we must doubt, even if he had done it, the validity of means and variabilities based upon two to four individuals. Still his memoir is very suggestive, and it seems to me that the investigation of a large series of head measurements in parents, and, if possible, adult children, say, in 1000 families forming a homogeneous population, would be of great value.

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[*] I have shown in 'Biometrika,' vol. 1, p. 399, that the values of the standard deviation found from two individuals will, on the average, only be about 0·563 of its true value. Similar large reductions occur if it be found from three to four individuals, and so on. This is quite apart from the large probable errors introduced by paucity of numbers.

[†] 'Roy. Soc. Proc.,' vol. 62, p. 394.

[‡] There would, I take it, certainly be correlation between $x - y$ and the omitted ancestral terms in the family mean.

(13.) The present paper has, I think, brought out the following points :—

(i) A variability criterion between contending theories of inheritance is possible, and is easily applied.

(ii) Variability plotted to parental character will give (*a*) a horizontal straight line on the Theory of Ancestral Heredity, (*b*) a parabola with axis along the axis of parental character on Mendelian Principles, (*c*) a hyperbola with its real axis perpendicular to the axis of parental character on the Theory of Alternate Inheritance which is summed up in the idea of parentally differentiated groups within the family.

(iii) As far as my own measurements on stature, span, forearm, and cephalic index in man go, there is nothing to support the view that the variation curve of (ii) is effectively represented by either a parabola or a hyperbola. Within the limits of the probable errors of random sampling it appears to be a horizontal straight line.

Further applications of the criterion will no doubt be soon forthcoming, but it is essential they should be made with a full understanding of what the various theories amount to, and how they must be applied to observations. In particular it is very needful that we should distinguish between the mean of an individual family as determined from all its ancestry, and the mean of an array of offspring of given parentage-type—but with all varieties of earlier ancestry—determined from that parentage only.